BLUE-GREEN ALGAE FROM THE MIDDLE DEVONIAN OF RHYNIE, ABERDEENSHIRE

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Pp. 339–353 ; *Plates* 41–44

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 3 No. 10
LONDON : 1959

* Deceased.

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 3, *No.* 10 *of the Geological series.*

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

Issued February, 1959 *Price Eight Shillings*

BLUE-GREEN ALGAE FROM THE MIDDLE DEVONIAN OF RHYNIE, ABERDEENSHIRE

By the late W. N. CROFT AND E. A. GEORGE

SYNOPSIS

Three new blue-green algae, *Langiella scourfieldi* nov. gen. et sp. (Stigonemataceae), *Kidstoniella fritschi* nov. gen. et sp. (Stigonemataceae) and *Rhyniella vermiformis* nov. gen. et sp. (incertae sedis) are described from the Middle Devonian Rhynie Chert Bed in Scotland. The material is well preserved and details of the sheath, cell wall, cell contents and heterocysts are clearly seen. It supports the view that the Myxophyceae are an ancient stock and indicates that the Stigonemataceae which are generally regarded as being among the most advanced members of the class existed as early as the Devonian age.

I. INTRODUCTION

SINCE the classical memoirs of Kidston & Lang (1917–21) on the vascular cryptogams and thallophytes of the Rhynie Chert Bed, no further work has been published on the plants of this deposit.

Archaeothrix (Kidston & Lang, 1921) is the only fossil so far described from this chert which could reasonably be placed within the blue-green algae. The material on which the present account is based confirms the presence of Myxophyceae in the deposit and adds very materially to the knowledge of the fossil history of this important group of plants.

The specimens, placed in three new genera, occur in a single small chip of the chert. This was found labelled " ? Blue-green alga " in D. J. Scourfield's collection which was bequeathed to the British Museum (Natural History) in 1950.

The rarity of remains of blue-green algae in the deposit is in contrast with the abundance of other plants, especially fungi. It is the more striking when it is remembered that these algae are generally abundant at the present day in warm springs in which siliceous material is being deposited. It suggests that the habitat was little favourable to their growth, but is in no way contradictory to the well founded view that the peat bog was overwhelmed by flooding (Kidston & Lang, 1921 : 892).

The method adopted for studying the plants in the chip was that used by Scourfield (1926 : 154) for the crustacean remains ; direct examination in oil with an oil-immersion objective. Examination and illustration of the plants are rendered difficult by the thickness of the chip and the amount of debris contained in it. It was often necessary to readjust the setting of the substage mirror even for examination of different parts of the same plant. Moreover the cell walls often contrast little with the matrix and the outlines and visibility of the cells and of the sheaths vary considerably with the setting of the mirror and the width of the illuminating cone.

II. DESCRIPTION OF THE MATERIAL

The chip is about 1 mm. thick and nearly 5 mm. across. The topography of the two sides is shown at a magnification of × 14 in Pl. 41, figs. 1, 2. In the upper right-hand corner of fig. 1 numerous trichomes of *Langiella*, including the type specimen, are present. They tend to be similarly orientated (Pl. 43, fig. 17). Numerous trichomes of the same species are seen in the same corner of the chip from the other side (Pl. 41, fig. 2), but they are not aligned. Near the middle of the upper edge of the chip (Pl. 41, fig. 1) is the only specimen of *Rhyniella*. Associated with it are a few filaments of *Langiella*. Running obliquely through the lower right-hand portion of the chip in Pl. 41, fig. 2 is part of what is presumed to be a vascular axis about 1·4 mm. in diameter. Along the edge of this axis and partly detached from it is a narrow zone of trichomes of *Kidstoniella*. As suggested below (p. 348) the plant probably grew epiphytically upon this axis. A few trichomes showing branching, near the middle of the face of the chip (Pl. 41, fig. 1) may belong to the same species. Many fragments of plant tissue are present together with abundant fungal hyphae. These latter are occasionally branched and rarely septate. Spores have not been observed.

The occurrence of these three species in such close proximity is not unlike present-day communities of Myxophyceae. Mats and cushions consisting of several species or genera almost inextricably interwoven are a characteristic covering of damp surfaces to-day.

That so much has been learnt of the algal flora of the Rhynie Chert from one small chip encourages the hope that further fortunate discoveries may add still more to our knowledge.

III. SYSTEMATIC DESCRIPTIONS

MYXOPHYCEAE

Order STIGONEMATALES

Family STIGONEMATACEAE

Genus ***LANGIELLA*** nov.

Diagnosis. Mature thallus heterotrichous. Prostrate axis multiseriate, cells large and moderately thick-walled with both transverse and longitudinal divisions, also rounded cells in small aggregations, branches few, heterocysts absent, sheaths thin. Erect filaments essentially uniseriate, unbranched, trichomes more or less strongly torulose, cells generally smaller and except in the proximal region of some filaments, thinner-walled than those of the prostrate system; sheaths generally thin, but thicker in middle and upper parts of some filaments; in the upper parts of some filaments trichomes much narrower with more elongate cells or no clear evidence of cell walls; ends of some filaments multiseriate with cells formed by oblique divisions. Heterocysts, at or near the base of most erect filaments, absent from the basal system, walls refractive, contents depleted, shape subspherical to cylindrical. Reproduction by fragmentation of erect filaments at heterocysts, probably by single akinetes formed in basal system, possibly by catenate akinetes formed in lower part of erect filaments, possibly by hormogonia released from the tips of erect filaments.

Diameter of prostrate axes, 22 μ to 40 μ ; diameter of prostrate axes cells, 12 μ to 20 μ.

Length of erect filaments about 100 μ to 300 μ.

Maximum width of trichome (lower part), 16 μ. Minimum width of narrowest trichome, 8 μ.

Length of heterocysts, 6 μ to 10 μ ; width 6 μ to 8 μ.

TYPE SPECIES. *Langiella scourfieldi* n. sp.

Langiella scourfieldi n. sp.

(Plate 41, figs. 1, 3–8, 10 ; Pl. 42 ; Pl. 43, figs. 17, 19–24)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.)

OCCURRENCE. Middle Devonian (Old Red Sandstone) ; Muir of Rhynie, Aberdeenshire, Scotland.

General morphology. The holotype (Pl. 41, fig. 10 and Pl. 42, fig. 12) is markedly heterotrichous and the same habit is indicated by some of the obscurely seen specimens alongside it (to the left in Pl. 41, fig. 1). A multiseriate basal system, curved round into the shape of an asymmetrical horse-shoe, gives rise on its outer edge to a number of uniseriate branches. Most of these, including two or three apparently detached filaments are subparallel, similarly orientated and lie in almost the same plane. Some at least of the uniseriate branches were probably fertile. Possibly the basal system was originally more or less straight and creeping with erect branches arising on the side opposite the substrate. Most of the specimens in the chip are, however, clearly unattached and there is no direct evidence that they ever were attached to a substrate. A description of a few associated forms follows that of the holotype (p. 346).

Basal system. The compacted cells of the basal system are generally broader and thicker-walled than those composing the erect filaments. They are not arranged in regular transverse rows as is usually the case in present-day species of *Stigonema.* The left-hand portion of the basal system (Pl. 41, fig. 10) attains a thickness of about 40μ. A row of broad thick-walled cells formed by transverse and longitudinal divisions, up to 18 μ across, is clearly seen on its surface. Beneath these, at a deeper focus, a few small cells with polygonal outlines suggesting mutual pressure are visible. The dense right-hand portion shows a row of three large thick-walled cells 20 μ in diameter. The middle, curved portion of the basal system consists of rounded cells one of which with a thick wall and a diameter of about 18 μ is suggestive of an akinete (Pl. 42, fig. 12). Some of the cells of the basal region may be " chroococcoid ", but this is uncertain ; heterocysts seem to be quite absent from the basal system.

Branches Nos. 12 and 14 (Pl. 41, fig. 10) are dark like the basal system and are probably branches of it. Unlike the erect branches they are crooked and lack heterocysts. The status of branch No. 1 is uncertain. The cells are rather short in branch No. 12 and a few of them are wedge-shaped. The distal portions of branches Nos. 1 and 14 are narrow and composed of elongate cells similar to those of the hair-like terminations of a few of the erect branches.

Erect system.—The erect filaments of *Langiella* are quite unbranched and essentially uniseriate. Though generally curved or slightly sinuous they give the appearance of being somewhat rigid. The longest filament measures about 300 μ.

The cells of the filaments present some diversity of size and shape. Many of the cells are slightly wider than long, others nearly twice as broad as long, while others are depressed globose, cask-shaped or truncate ovoid. In some filaments there are cells once to twice as long as broad, wedge-shaped cells also occur. The small cells which are clearly heterocysts also show a diversity of form ; they are described in detail below (p. 345). The trichomes are generally markedly torulose and may be nearly moniliform. The two short branches, Nos. 4 and 9, are of nearly uniform width throughout and the end cells are subspherical. The larger branches, however, show a more or less clear differentiation into a proximal portion resembling these two branches and a distal portion which usually has an elongate cell at the base. The distal portions are of two main types. In one type it is hair-like and slightly club-shaped with comparatively long and narrow cells giving the whole branch a somewhat tapering form, e.g. Nos. 2 and 5. The other type is composed of cells which are shorter and thinner-walled than those of the proximal portion and the apex may include a few rather large cells or cells formed by oblique divisions, e.g. Nos. 3 and 7. There is a tendency for the end cells of all the filaments to be somewhat longer than the penultimate cells and they are always rounded, never pointed or attenuate. The sheath surrounding the proximal part is thin, usually fairly dark and well defined and often slightly torulose. That around the distal cells, however, is less distinct but thicker and at the thickest part the width of the filament may be nearly twice that of the trichome (Pl. 42, figs. 13, 15).

Basal portion of erect filaments. The catenate basal cells of some of the erect filaments are large and torulose with well-defined walls and a dark narrow sheath. A good example of this is seen in branch No. 8 (Pl. 42, fig. 12) where the basal heterocyst is succeeded by a row of seven cells which contrast rather sharply with the less well-defined, less torulose and generally smaller cells of the distal portion. These proximal cells have a diameter of about 10 μ and those of other filaments from 9 μ to 12 μ. They recall the lower cells of the uniseriate filaments of certain Rivulariaceae, lying next to the heterocyst which as in the fossil is not enclosed in the sheath. In filament No. 11 the four cells lying between the two heterocysts are unusually large and well defined, and the dark sheath closes round the end cells. The largest has a diameter of 13 μ. It is possible that these are resting cells (akinetes) as developed in e.g. *Nodularia.* They may, however, merely be thick-walled older cells like those met in the filaments of *Stigonema* and *Hapalosiphon.* If they are resting cells it seems possible that the basal cells of some of the other filaments may be incipient akinetes.

Distal portions. The modifications shown by the distal portions of the filaments have already been briefly noted. The hair-like form is well shown in filament No. 11 (Pl. 42, fig. 15) in which the end four cells are considerably smaller, though unchanged in shape, giving a sudden reduction by about one-third in the width of the trichome. The basal cell of the four is subcylindrical and about twice as long as broad, whereas the remaining cells are subspherical. The hair-like terminal portions of branches

Nos. 2, 5 and 10 also have elongate basal cells and increase slightly in width towards the apex where two or three rounded cells can be faintly seen. The cells in the middle part of the trichome are long and attenuated. The sheath around these latter trichomes is very faintly seen and is narrow, whilst that of filament No. 11 is more distinct and also wider.

Branch No. 3 is an example where the trichome does not end in a hair-like portion. The swollen apex which follows after a series of rather small cells with indistinct walls, consists of perhaps six or eight cells formed partly by oblique divisions. Their walls are not all distinct and it is impossible to say whether any of them are ruptured. The sheath around the terminal portion of the trichome which is separated from the proximal portion at an intercalary heterocyst is ill-defined but apparently of moderate width. The last few cells of branches Nos. 6 and 7 include some wedge-shaped sublateral cells probably indicating an early stage in the development of a multicellular termination like that of branch No. 3. However there is a rather similar wedge-shaped cell at the proximal end of branch No. 10 which can hardly be interpreted thus. At the end of branch No. 13 a short length of trichome, about 35 μ long with five rather ill-defined partitions, appears to be detached from the rest of the filament and to be emerging from the end of the sheath (Pl. 42, fig. 14). Its maximum width (13 μ) is somewhat greater than that of most of the trichome. Proximal to it is a shorter piece of trichome, apparently consisting of two cells, which is similar to that near the end of filament No. 8. It is possible that these pieces of trichome, especially the first, had a propagative function like that of hormogonia.

The sheaths of filaments Nos. 8 and 13 are rather wide and increase gradually and markedly in width from the lowest cell of the terminal portion of the filament as is well shown in Pl. 42, fig. 13. A similar contrast between the sheaths of the basal and of the terminal portion is shown by branch No. 11. In each of these three filaments the sheaths taper both proximally and distally and the widest part, where the filament is nearly twice the width of the trichome, occurs nearer to the apex than to the base. The hair-like termination of filament No. 11 is enclosed by the sheath. In filament No. 8 (Pl. 42, figs. 13, 16) and more clearly in the isolated piece of trichome shown in Pl. 43, fig. 23 there are indications of dark, more or less transverse lines or bars in the sheath, the only indications of lamination to be observed.

Heterocysts. All the erect filaments, with the possible exception of No. 10, have a heterocyst at or near the point of origin of the filament from the prostrate system. In two branches (Nos. 3 and 11) there is also a second, intercalary, heterocyst near the middle of the branch. The basal heterocyst is usually more or less symmetrically placed in relation to adjoining cells. In filament No. 4, however, the heterocyst is somewhat wedge-shaped and in a rather lateral position. The heterocyst may be ovoid to cylindrical, spherical or subquadrate, the long axis is usually parallel to that of the trichome. Examples of cylindrical trichomes are seen in filament No. 2 and in the isolated piece of filament shown in Pl. 43, fig. 24. These heterocysts, which are always distinctly smaller than the adjoining cells, range in diameter from 5 μ to 8 μ and in length from 5 μ to 10 μ. In several instances the heterocyst is broader and flatter at the proximal pole. The heterocysts are characterized chiefly by the hyaline nature of the wall, giving the appearance of a thin bright line. As may be seen in Pl. 43, fig. 22, the inner boundary of the wall is defined by a dark line, perhaps formed by deposits on the wall. The outer boundary of the wall is more faintly demarcated. In no case does the heterocyst appear to be enclosed in the sheath. The absence of a sheath would no doubt facilitate fragmentation of the trichome at the heterocyst. That fragmentation did occur is clearly shown by the isolated filament in Pl. 43, fig. 23 and by filament No. 2. This last example suggests that fragmentation normally took place distal to the heterocyst and this is supported by the observation that the distal end of the heterocyst is more often pointed than the other. Branch No. 6 which has no basal heterocyst was quite possibly detached in this way. The isolated filament in Pl. 43, fig. 24 shows that the heterocyst may permit considerable displacement of the filament without fragmentation occurring.

Cell contents. In some cells of a few branches of the erect system there are indications of cell contents. These consist of slightly darker central areas with a defined, rounded outline which often follows the outline of the cell wall. These areas appear minutely granular. The diameter is usually less than half that of the containing cell. In several examples the area lies slightly to the left of the centre. In a cell near the middle of filament No. 6 the faintly granular contents are but slightly contracted away from the cell wall and there are also signs of partial contraction in the cell next but one below it. The prominent black dendritic contents in branch No. 4 (Pl. 43, fig. 19) largely disregard the boundaries between the cells. It is probable that these, like the irregular black markings in a few other cells of the plant (Pl. 42, figs. 12, 15, 16) are merely inorganic, probably pyritic, deposits like those scattered through the matrix.

The heterocysts are scarcely paler than most of the other cells of the filaments. A few of them have irregular black deposits on the inner side of the wall. The example illustrated in Pl. 43, fig. 19 is the only heterocyst to show clear indications of a central dark area. This also may be inorganic.

It should be noted that in *Archaeothrix* Kidston & Lang (1921 : 875) from the same geological deposit the cell contents are also preserved.

Other specimens of Langiella. Closely associated with the holotype and clearly belonging to the same species are numerous filaments, few of which can be seen clearly. Most of them are uniseriate. A few are straight uniseriate filaments with heterocysts like those of the erect system of the holotype (Pl. 43, figs. 23, 24). The majority are more or less crooked (Pl. 41, figs. 3, 6, 7 ; Pl. 43, figs. 20, 21) and resemble branches Nos. 12 and 14 of the holotype which are regarded as vegetative branches of the prostrate system. They include small intercalary cells which, because of their size, are possibly incipient heterocysts. But they lack the distinctive characters of those of the erect system, especially a hyaline wall and elongation parallel to the axis of the filament. Also they are more or less clearly enclosed in the sheath, which is usually rather well developed. A few of the cells show cell contents as a dark central area, as in the holotype. These additional specimens do not include any cells which can definitely be recognized as akinetes or hormogonia and do not give any further evidence as to the methods of propagation or of the growth of the plant. They do, however, provide additional evidence of the modes of cell division and of branching.

The smallest group of cells seen, consisting of a row of three cells of graded size with a definite sheath, is shown in Pl. 41, fig. 5; whether they were formed by germination of a spore or by fragmentation is uncertain. Pl. 41, fig. 8 shows a short row of rather wide cells up to 16 μ in diameter. The small basal cell, which does not appear to be enclosed in the sheath is probably a heterocyst. Of particular interest is the fact, clearly demonstrated by focussing at different planes, that the distal cell has undergone a longitudinal division, and one of the daughter cells is further divided in a plane at right angles to the previous division. The piece of filament in Pl. 41, fig. 4 shows at its widest part a pair of collateral cells, presumably formed by division of an apical cell rather than by longitudinal division of an intercalary cell. The bent piece of filament in Pl. 41, fig. 7 shows a small cell at the bend formed by oblique division. The specimen in Pl. 41, fig. 6 and Pl. 43, fig. 21 appears to consist of two short filaments crossing one another. The large dark-walled cell near the centre may possibly be an akinete which has germinated. Lastly in Pl. 41, fig. 3 the upper filament appears to be branching out of the more horizontal filament. The downwardly directed filament appears to originate at the junction of the filaments. The upper filament shows what is perhaps an incipient heterocyst where the filament bends.

DISCUSSION. As is general in the filamentous blue-green algae, the cell division in *Langiella* is predominantly transverse. In the Stigonematales, where true branching occurs, the branches arise from the longitudinal division either of an apical cell or of an intercalary cell. Branches produced in this latter way push through the sheath of the filament and increase in length by the usual transverse divisions. In the holotype and the other fossil material examined this type of longitudinal division of an intercalary cell is nowhere conclusively shown. Presumably such must have occurred both to increase the thickness of the prostrate axis and to produce the numerous erect filaments arising from it. It is considered unlikely though not impossible that all these arose from apical cells.

Elongation of the erect filaments was probably in part at least from intercalary divisions in the distal portion of the filaments. In branches Nos. 3, 7 and 8 a series of short cells suggests recent cell divisions, such cells are not found in the proximal, presumably older, parts of the filaments. The subterminal lengths without cross-walls in filaments Nos. 2, 5 and 10 recall the filaments of Recent species of *Fischerella* (Geitler, 1932, text-figs. 296–299) where hormogonia are in the process of leaving the sheath of the parent filament. However it seems that this is not the case here, as the non-septate portion appears not to be an empty space but more like an attenuated cell. The possibility of necrotic lengths of trichome must also be considered, especially as Kidston & Lang (1921 : 835) report necrotic and wound areas in *Rhynia*.

An interesting feature clearly shown by the holotype and other specimens is the prevalence of wedge-shaped cells, often small and lying at a bend of the filament; they were presumably formed by the oblique division of an apical or perhaps an intercalary cell. This is especially well shown by the ends of branches Nos. 6 and 7 in the holotype where several cells are cut off by oblique walls.

Genus *KIDSTONIELLA* nov.

DIAGNOSIS. Thallus heterotrichous, epiphytic. Basal system consisting of a mass of cells, some of which are polygonal, forming thin parenchymatous tissue, others larger, rounded and thicker-walled. Erect branches uniseriate, straight, more or less strongly torulose, once or twice unequally branched by longitudinal division of the apical cell, or unbranched. Intercalary transverse divisions rare or absent. Cells variable in shape and size, mostly somewhat wider than long, end cells subspherical. Sheath seldom well preserved. Heterocysts small, nearly spherical, intercalary in erect filaments. Cell contents conspicuous in many cells of the thallus. Method of reproduction uncertain.

Cells of pseudoparenchymatous tissue of basal system 10 μ to 14 μ broad ; large rounded cells of basal system 16 μ broad ; erect filaments up to 160 μ long and up to 24 μ broad ; length of mature cells 5 μ to 14 μ ; heterocysts 5 μ to 6 μ long and 6 μ to 7 μ broad.

TYPE SPECIES. *Kidstoniella fritschi* n. sp.

Kidstoniella fritschi n. sp.

(Pl. 41, figs. 2, 9 ; Pl. 44)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.).

OCCURRENCE. Middle Devonian (Old Red Sandstone) ; Muir of Rhynie, Aberdeenshire, Scotland.

GENERAL MORPHOLOGY. As noted above (p. 342), this species appears to have grown epiphytically. Pl. 44, fig. 29 shows a dark band of multiseriate filaments forming a basal layer lying parallel to, but partly detached from the edge of an oblique section through a nearly opaque plant axis. A number of uniseriate filaments, a few of which are branched, arise from this basal layer and stand away from it at a wide angle. It seems likely that the axis, perhaps growing more or less erect, formed the substrate for the heterotrichous thallus of the alga.

Basal system. Much of the basal system shown in Pl. 41, fig. 9 is composed of a dense mass of rather ill-defined cells. Some of these are rather large, spherical or ovate, with thick walls and clear indications of dark rounded contents. These cells attain a diameter of 15 μ. In part of the basal system a number of cells which are smaller than those forming the erect filaments have become polygonal through mutual pressure and form a thin pseudoparenchymatous tissue which in part at least seems to be monostromatic. Another part of the basal system is formed of imperfectly seen rounded cells up to 16 μ in diameter. There is little or no evidence of any mucilaginous sheath around the basal system.

Erect system. The more or less erect branches are essentially uniseriate and often strongly torulose. The cells vary considerably in shape and size. They are mostly somewhat wider than long, and may be twice as wide as long, ranging in shape from discoid or wedge-shaped to depressed—or truncate-globose. A few are slightly longer than wide, cask-shaped or ovoid. The end cells are rounded and when mature, subspherical. The filaments range in width from about 8 μ to 14 μ. An unusually large cell in filament No. 1 is 15 μ in diameter.

A feature of special interest is the unequal dichotomous branching shown by two of the erect filaments. In filament No. 1 the two divisions are but slightly divergent. The shorter and narrower division consisting of shorter but more numerous cells, is less developed than the other. In filament No. 2 the very short right-hand division is indistinctly preserved but appears to be multiseriate. The terminal cell of the left-hand division is itself divided by a faint but definite longitudinal wall (Pl. 44, fig. 27). From the fortunate preservation of the filament at this stage of growth it may be inferred that the other dichotomous divisions have also resulted from the longitudinal division of an apical cell. There is no clear indication in the thallus of the longitudinal or transverse division of an intercalary cell and it might therefore be concluded that growth was wholly apical. However, in filaments Nos. 1 and 4 there are rather short cells which might be products of recent intercalary divisions. The large end cell of filament No. 2 seems to be in process of dividing longitudinally, for the contents consist of two rounded bodies in place of the usual one. In the left-hand filament in Pl. 44, fig. 25 the distal end of the filament is divided into a number of imperfectly seen cells somewhat reminiscent of the multicellular tips seen in *Langiella*. The large end cell of the next filament seems to be in the process of dividing longitudinally for two rounded bodies are seen inside it. Springing from the right-hand side of this filament is a short club-shaped body whose contents are divided into three or four very small portions not obviously separated by septa. This appears to be an incipient branch and may be compared with the branch of very short cells in filament No. 1. The pair of cells just below the branch in filament No. 2 may have resulted from a transverse intercalary division.

The erect filaments have few and discontinuous pieces of a surrounding sheath. The clearest examples are round the distal parts of filaments Nos. 2 and 3 and around filament No. 4.

Heterocysts. The small nearly spherical cells indicated in filaments Nos. 3 and 4 are possibly heterocysts. Their diameters are about 6 μ. Like those in *Langiella* they are small and have a hyaline wall delimited by dark lines of which the inner seems to be the darker. A few of the normal sized cells, for instance those on each side of the heterocyst in filament No. 4, also have hyaline walls, though in these the outer limiting line seems to be the darker. Most of the cells having a thin dark wall in optical section, show a similar shining wall at a slightly higher focus. In shape and appearance these two cells resemble the small intercalary cells thought to be heterocysts in some of the filaments of *Langiella*.

In Pl. 44, fig. 27 several of the cells, notably in filament No. 3, show a clear wall bounded internally by a fine dark line. The small intercalary cell in this filament recalls by its size the cells which are regarded doubtfully as heterocysts in filaments of *Langiella*. The wall, however, is not hyaline, cell contents are present and the sheath appears to enclose it. This may well be an example of a small cell which has not yet developed into a heterocyst.

Cell contents. In most of the cells in the uniseriate filaments, as well as in the basal region, there are more or less clear indications of contents (Pl. 44, figs. 27–29).

As in *Langiella*, these consist of darker, central areas with a rounded outline. As a rule the larger bodies are found in the larger cells. The shape of the central area corresponds generally with that of the cell, being wedge-shaped in wedge-shaped cells and transversely elongate in discoidal cells. The central areas are particularly well defined in the distal regions of filaments Nos. 1 and 2. In the main division of branch No. 1 the central areas of four cells are more or less sharply delimited and surrounded by a narrow clear zone or halo which is paler than the outer zone. In certain cells in filament No. 2 the clear zone appears to be delimited from the outer, slightly dark, contents of the cell by a fine line. This suggests that the zones outside the central dark area may represent mucilaginous or other contents of the cell. With the highest resolution which could be used the dark central areas appear to be finely granular. The cell immediately below the dichotomy in filament No. 1 appears to be empty and to be ruptured on its left side.

MYXOPHYCEAE

INCERTAE SEDIS

Genus ***RHYNIELLA*** nov.

DIAGNOSIS. Thallus filamentous, essentially uniseriate, vermiform, non-heterotrichous. Trichomes mainly sinuous within a mucilage sheath, often two or three sharing a common sheath, branching doubtful, heterocysts doubtful, some with multicellular apices. Cells usually broader than long, wedge-shaped at the sharper bends in the trichome. Terminal cells rounded or rarely bluntly pointed. Method of reproduction unknown.

Trichome up to 140 μ long ; cells 4 μ to 10 μ long and 10 μ to 14 μ broad.

TYPE SPECIES. *Rhyniella vermiformis* n. sp.

Rhyniella vermiformis n. sp.

(Pl. 41, figs. 1, 11 ; Pl. 43, fig. 18)

DIAGNOSIS. As for genus.

HOLOTYPE. Specimen No. V.32409, Palaeont. Dept. Brit. Mus. (Nat. Hist.).

OCCURRENCE. Middle Devonian (Old Red Sandstone) ; Muir of Rhynie, Aberdeenshire, Scotland.

GENERAL MORPHOLOGY. The species represented in Pl. 41, fig. 11 is found near the middle of the upper edge of the chip in Pl. 41, fig. 1 and does not appear to be present elsewhere in the chip. It consists of numerous subparallel trichomes many of which are distinctly vermiform. The drawing is considerably condensed, but the thickness of the bundle of trichomes is much less than the width. The cells are typically broader than long ; wedge-shaped cells are found at the sharper bends in the trichome. Several trichomes are more or less isolated and enclosed in their own sheaths. Some of the trichomes, however, are closely associated for part of their length and it is practically certain that they share a common sheath. No clear case of branching has been observed. Nor are heterocysts certainly present, though one cell may be of this type.

There is no defined basal system ; the multicellular, and presumably distal, terminations of many of the filaments are, however, with one exception similarly orientated and the direction of growth was probably to the right in Pl. 41, fig. 11.

Trichomes. Some of the more distinct trichomes attain a length of 140 μ, and vary in width from 10 μ to 14 μ. A few of the indistinctly seen trichomes are nearly straight, but the majority are sinuous, and a few are bent at right angles. All but the terminal cells are shorter than wide and many are twice as wide as long. At the bends in the trichome the cells are more or less markedly wedge-shaped, in some instances not reaching across the full width of the trichome. There are generally distinct constrictions at the septa. The end cells vary considerably in shape, they may be segmental, hemispherical, subspherical or spherical. If spherical two or more may form a group. A few of the hemispherical cells are bluntly pointed. At A (Pl. 41, fig. 11) a trichome is terminated by an unequal pair of rounded cells : and at B the penultimate cell is divided longitudinally. At C an unusually large, oval-shaped end cell (length 20 μ ; breadth 14 μ) appears to be dividing. The various groups of terminal cells may have had a propagative function.

To the left of the centre of Pl. 41, fig. 11 there is a small cell almost surrounded by a curved piece of trichome. This cell is subquadrangular and measures 5 μ by 6 μ. It is distinctive not only because of its size and shape but because the wall is hyaline and marked on its inner boundary by a heavy dark line. These features characterize those cells of *Langiella* which are confidently regarded as heterocysts ; this cell must therefore be regarded as quite possibly a heterocyst. Its position in the thallus is, however, unusual and its true nature is uncertain.

Some of the trichomes are divided into lengths composed of from 4 to 12 cells. The longest piece of trichome without such a segmentation has 18 cells. The end cells of each segment are usually hemispherical or subspherical. There may be a small, nearly spherical cell connecting two segments as in the central trichome in the lower part of Pl. 41, fig. 11. These small cells do not have a hyaline wall.

In a few places, the trichomes are closely parallel for part of their length indicating that they share a common sheath. The mode of branching, if this does occur, is not clearly demonstrated at any point.

Cell contents. As indicated in Pl. 41, fig. 11 a few of the cells show rounded contents. Though indistinct, they do not appear to differ significantly from those in the associated species.

Sheaths. The trichomes are enclosed in more or less clearly defined sheaths which vary in thickness from a quarter to a half of the trichome width. In one or two places where the edge of the sheath is clearly defined it is irregularly sinuous. The sheaths also show indications of longitudinal folds. Two of the more isolated trichomes are completely enclosed in their own individual sheaths. The majority of the trichomes appear to share a common sheath, at least over part of their length.

DISCUSSION AND COMPARISON. *Rhyniella* differs from the other two genera in the apparent absence of heterotrichy, of heterocysts and in its shorter and less rounded cells. It calls to mind forms like *Tolypothrix elenkinii* and *Scytonema* (*Diplocolon*) *crustaceum* (Geitler, 1932 : 738, 784). Both these Recent species are heterocystous and non-heterotrichous with many contorted trichomes in a common sheath. However the possibility must not be overlooked that this specimen grew from a basal system which is not now in evidence. From its general appearance and cell morphology it could not be part of either *Langiella* or *Kidstoniella* which, however, it resembles in the possession of multicellular apices. Nothing quite like these structures occurs in present-day members of the class.

IV. CONCLUSIONS AND GENERAL DISCUSSION

It is now evident that in Middle Devonian times the blue-green algae had reached an evolutionary grade which is generally regarded as advanced among Recent forms, namely a heterotrichous thallus with a pseudoparenchymatous basal system. The enigma of the heterocyst, so well presented by Fritsch (1951) is no nearer solution, but it is clear that the evolutionary origin of the heterocyst must be sought in still older fossils.

The multicellular tips to the trichomes seen in *Langiella* and *Rhyniella* and rarely in *Kidstoniella* are of considerable interest in that they have no close parallel in present-day forms. Rather similar structures in *Stigonema dedroideum* were described by Frémy (1930) as conidia, but there the cells are rounded and separated within mucilage. It is of course possible that the fossil structures are an early stage, either phylogenetically or ontogenetically, in the development of such conidia.

There is a certain similarity in general appearance between *Langiella* and *Kidstoniella* but it is considered most unlikely that they belong to the one species or even the same genus. *Langiella* has unbranched erect filaments with distinct heterocysts and occasional multicellular tips, while *Kidstoniella* shows true branching of the erect filaments which have few multicellular tips and doubtful heterocysts. How constant these characters were in the living population one cannot say but on the present evidence and in accordance with taxonomic practice, both in phycology and in palaeobotany they must be considered separate genera. There can be little doubt that these two genera belong in the Stigonematales (Geitler, 1925; Fritsch, 1942) and there are no characters on which one could satisfactorily found a new family apart from the Stigonemataceae.

The position of *Rhyniella* is less certain. On the present probably incomplete evidence it is non-heterotrichous and unbranched, suggesting a position in the Nostocales (Geitler, 1925 ; Fritsch, 1942) and perhaps within Oscillatoriaceae but the presence of multicellular tips as in *Langiella* suggests Stigonematales and possibly a close relationship with *Langiella*. This difficulty in assigning a taxonomic position to a blue-green alga is by no means limited to fossil forms ; there is wide lack of agreement over the classification of present-day forms (see Papenfuss, 1955).

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PLATE 41

Langiella scourfieldi, *Kidstoniella fritschi* and *Rhyniella vermiformis*

FIG. 1. Drawing of the chip showing position of the fossils, in particular *Langiella scourfieldi* (top right-hand corner) and *Rhyniella vermiformis* (centre). × 15 (V.32409).

FIG. 2. The same, reverse side, to show position of *Kidstoniella fritschi*. × 15.

FIGS. 3–8. Drawings of isolated filaments of *Langiella scourfieldi* associated with the holotype. × 280.

FIG. 9. Drawing of the holotype of *Kidstoniella fritschi* constructed from photographs and direct observation. × 280.

FIG. 10. Drawing of the holotype of *Langiella scourfieldi* constructed chiefly from photographs at different focal levels, but partly from direct observation. × 280.

FIG. 11. Drawing of the holotype of *Rhyniella vermiformis* from photographs and direct observation. × 280.